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THE CAMBIUM AND ITS DERIVATIVE TISSUES II. SIZE VARIATIONS OF CAMBIAL INITIALS IN GYMNOSPERMS AND ANGIOSPERMS

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INTRODUCTION

Much has been written during the last fifty years concerning the relations between cell size, and body size, nuclear size, chromosomal number, and chromosomal mass. One group of botanists and zoologists, including such classical writers as Sachs (1893), Driesch (1898, 1900), and Boveri (1904), maintain that the size of the cells in specific organs or organisms remains constant regardless of variations in growth or stature, whereas another group hold that cell number rather than cell size is fixed. A second controversy revolves around the question whether the nucleo-cytoplasmic relation is a constant or a self-regulating ratio, and, more recently, whether dwarf and giant mutants are produced by changes in the number or in the size of chromosomes.

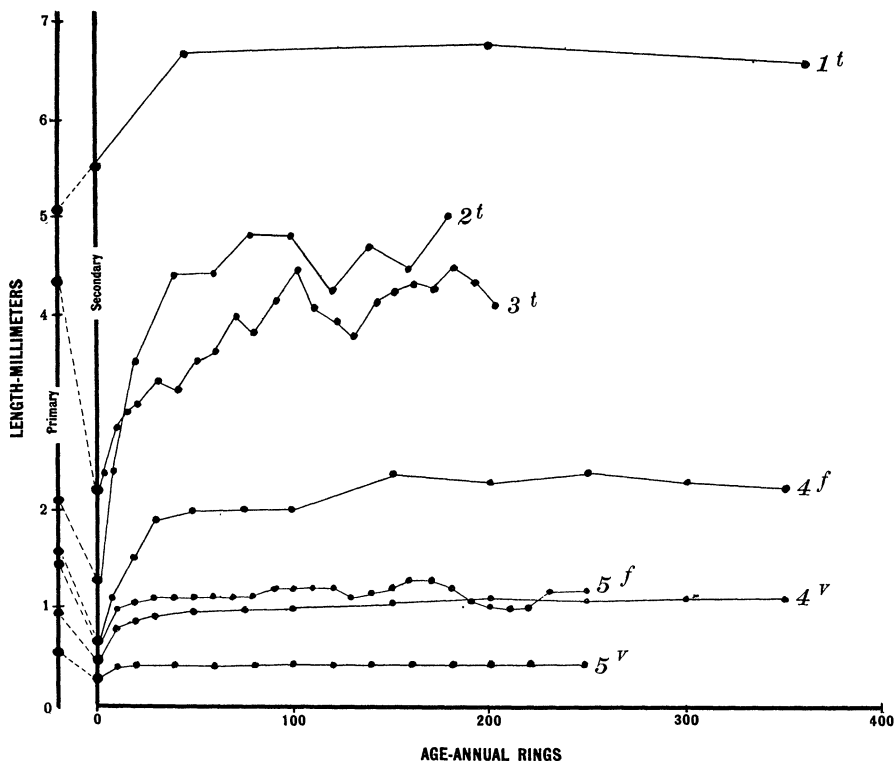
Many of the discrepancies in the conclusions of these writers appear to be due to an intensive study of a particular tissue, organism, or stage in ontogeny without reference to what may occur in other tissues, organisms, or developmental stages. Levi (1906) has shown that in mammals the size variations of epithelial and gland cells—elements which continue to divide throughout life—are insignificant, whereas such highly differentiated cells as nerve fibers, lens fibers, muscle fibers, and ganglion cells tend to be considerably larger in large animals than in small ones. Thus, the necessity for *extensive* preliminary, comparative investigations in selecting material for *intensive* experimental research, and to serve as checks upon excessive generalization from limited induction, is well illustrated by the literature dealing with body size and cell size.

In the first investigation of this series¹ an attempt was made to determine, by means of an extensive reconnaissance survey, what are some of the more fundamental types of size variations that occur in the tracheary

¹ Bailey, I. W., and Tupper, W. W. Size variation in tracheary cells: 1. A comparison between the secondary xylems of vascular cryptogams, gymnosperms and angiosperms. Proc. Amer. Acad. Arts and Sci. 54: 149-204. 1918.

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cells of the secondary xylem of vascular plants. The elements were found to fluctuate considerably in length in different parts of an organ or plant, in individuals grown under different environmental conditions, and in different groups of the Siphonogama. As shown in text figure 1, the average length of the tracheary cells, in a given radius and at a particular height in the stem of an arborescent dicotyledon or gymnosperm, is not constant

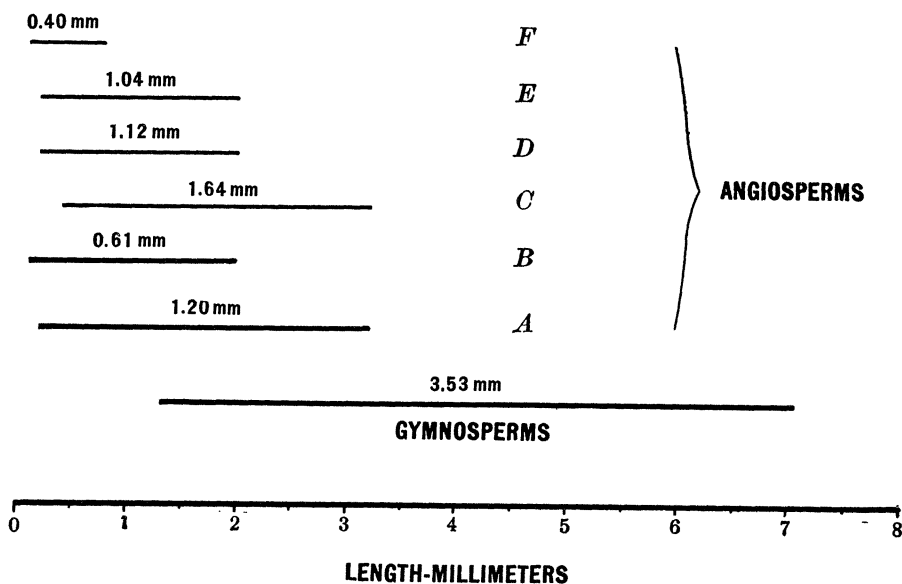


TEXT FIG. 1. Curves showing variations in average length of tracheary cells in passing from the innermost to the outermost secondary xylem of the stem. Average lengths of primary tracheary elements shown for comparison. 1, cycad; 2, conifer; 3, vesselless dicotyledon; 4, dicotyledon with primitive vessels; 5, dicotyledon with highly differentiated vessels. *t*, tracheids; *f*, fiber tracheids; *v*, vessel-segments. Modified from Bailey and Tupper.

in succeeding annual rings, but tends to increase rapidly for a period of years and subsequently to fluctuate more or less above and below a certain general level. This length-on-age curve varies in different portions of the stem and in plants grown under different environmental influences. In normal forest trees, its crest tends to be higher in the "clear length" of the stem and lower in the crown, in the stump, and in proximity to burls, severe injuries, and other disturbing factors. Although these somatic variations, due to physiological and ecological factors, are so varied and extensive as to render

difficult the isolation of germinal fluctuations in a limited number of closely related plants, the study of a wide series of Siphonogama reveals striking differences in the size of the tracheary cells in different groups of plants. For example, the average length of the tracheids in the outer rings of the secondary xylem of 152 gymnosperms was 3.53 ± 0.07 mm. ($SD = 1.25 \pm 0.05$ mm.); whereas in comparable material of 275 dicotyledons, from 31 orders and 118 families, the mean length of the fiber tracheids² and vessel-segments was 1.20 ± 0.02 mm. ($SD = 0.50 \pm 0.01$ mm.) and 0.61 ± 0.02 mm. ($SD = 0.41 \pm 0.01$ mm.) respectively (text fig. 2).

The reduced length of the tracheary elements in the secondary xylem of



TEXT FIG. 2. Limits of variability of average lengths of tracheids in the older wood of 152 gymnosperms contrasted with the limits of variability of (A) average lengths of fiber tracheids in older wood of 275 miscellaneous dicotyledons, (B) average lengths of vessel-segments in 275 miscellaneous dicotyls, (C) average lengths of fiber tracheids in older wood of 53 dicotyls having primitive vessels, (D) average lengths of vessel-segments in 53 primitive dicotyls, (E) average lengths of fiber tracheids in older wood of 169 dicotyls having highly specialized vessels, and (F) average lengths of vessel-segments in 169 specialized dicotyls. Mean of average lengths shown numerically.

dicotyledons appears to be closely correlated with the development and differentiation of vessels. This is indicated, not only by the striking general contrast between the sizes of the tracheary elements in plants which have vessels (Gnetales, dicotyledons) and in those which are devoid of them (vascular cryptogams, gymnosperms, vesselless^{*} Trochodendraceae, and

² Using this term in a general sense to include tracheids, fiber tracheids, libriform fibers, and septate fibers, but excluding substitute fibers.

Magnoliaceae, text fig. 1), but also by the fact that the tracheary cells in the dicotyledons tend to shorten as the vessels become more and more highly specialized (text fig. 2).³

In all of the arborescent dicotyledons and gymnosperms, with the probable exception of the Cordaitales, Bennettitales, and Cycadales, the first formed tracheary cells of the secondary xylem are relatively small and are considerably shorter than the adjoining elements of the primary xylem (text fig. 1). This is in marked contrast to the conditions which appear to have prevailed in the stems of many of the lower vascular plants. In forms having relatively wide zones of primary wood, the innermost secondary tracheids resembled in size the outermost primary tracheids. It seems probable that in the evolution of the higher gymnosperms and dicotyledons, with reduction in the amount of primary xylem and with other changes in the innermost portion of the stele, there has been a concomitant shortening of the first formed elements of the secondary xylem.

The size of the cells in the secondary xylem is determined by (1) the size of the cambial initials, and by (2) changes that take place in their derivative cells during differentiation into tracheary elements. It is conceivable, therefore, that the variations in the size of the tracheary elements may be closely correlated with similar fluctuations in the size of the meristematic cells. It is also conceivable, however, that the cells of the lateral meristem are of relatively uniform size, as hypothesized by Strasburger (1893), Winkler (1916), and others, and that the differences in the size of tracheary cells are due entirely to changes, *e.g.*, expansion, division, etc., which occur during differentiation of the xylem. The present paper is devoted to a comparative study of the size variations of cambial initials and tracheary cells.

MATERIAL AND METHODS

There are two methods of determining the sizes of the cells in a given tissue: by measurements taken (1) from sections and (2) from macerations. Each method has certain inherent advantages and disadvantages. In macerations it is possible to isolate individual cells and measure their various dimensions, but it is necessary to allow for differences in breakage,

³ The secondary xylem of the Calamariales, Sphenophyllales, Lepidophytineae, Cycadofilices, and Gymnospermae, exclusive of the Gnetales, is comparatively homogeneous, and its tracheary cells are of a single generalized type, so-called tracheids. In the Gnetales and Dicotyledoneae specialization or "division of labor" appears to have occurred among these cells. Certain vertical series of tracheids have become modified and function principally in conducting liquids, whereas others have assumed a mechanical rôle. As the vessels of the dicotyledons become more and more highly differentiated, their segments change their shape and structure and lose their resemblance to tracheids. At the same time, the surrounding tracheary elements tend to take on a more fiber-like structure, their pits becoming vestigial by the gradual disappearance of the bordering areas in the secondary walls.

shrinkage or contraction, etc. Of course, it is difficult to macerate the cambium and other soft tissues. The average length of vertically elongated elements may be obtained with a considerable degree of accuracy from longitudinal, tangential sections of tissues in which the elements are arranged in regular radial rows, *i.e.*, as in the cambium or xylem of gymnosperms. The lengths of the fiber tracheids and vessel-segments in most dicotyledons have to be obtained from macerations.

The measurements of the cells of conifers, recorded in the following table, were obtained from serial, tangential, longitudinal sections of the cambium and adjacent xylem, and were checked by measurements taken from macerations. In the case of the dicotyledons, the tabulated values were secured from tangential sections of the cambium and macerations of the outermost layer of the underlying xylem. The means are averages of fifty measurements, and their probable errors vary between 0.005 and 0.05 mm.

It is evident from these data that in *Ginkgo* and the *Coniferae* the length of the cambial initials closely resembles, but usually is slightly less than,⁴ that of the tracheids of the last formed growth layer of the xylem. In the dicotyledons, on the other hand, the meristematic cells are in most cases considerably shorter than the fiber tracheids, but are of approximately the same length as the vessel-segments. However, they tend to be slightly shorter than the vessel-segments in species (*Alnus*, *Euptelea*, *Myristica*, *Liquidambar*, *Rhizophora*, *Nyssa*) having primitive types of vessels, and a little longer than these cells in plants having highly specialized conducting systems. Therefore, by allowing for a 5–10 percent error, it is possible to use the tracheids of gymnosperms and the vessel-segments of arborescent and fruticose dicotyledons as indexes of the approximate length of the cambial initials in these two important groups of the vascular plants.

The principal types of size (length) variations that occur in the tracheary cells of the secondary xylem are closely paralleled by similar fundamental fluctuations in the longitudinal dimension of cambial initials. Thus, these meristematic cells vary in different parts of a plant or organ, in individuals grown under different environmental conditions, and in different groups of the *Siphonogama*. They are relatively short in young shoots and twigs of *Ginkgo* and *Coniferae*, but during subsequent growth increase in length for a period of years until a certain size level has been attained, after which they fluctuate more or less in response to various physiological and environmental influences. In comparable material, the normal length-on-age curve for the cambial initials tends to be considerably lower and flatter in the dicotyledons than in the conifers, and in plants having highly differentiated vessels⁵ than in those in which the conducting systems are relatively primitive (text fig. 3, page 363).

⁴ Mischke's (1890) calculations of elongation are based upon an erroneous premise, as has been pointed out by Klinken (1914).

⁵ In certain highly specialized dicotyledons the length of the short cambial initials, vessel-segments, and substitute fibers may remain constant or nearly constant during successive increases in the circumference of the stem, as suggested by Sanio (1873–74).

TABLE I.
Comparative Lengths of Tracheary and Meristematic Cells
GYMNOSPERMAE

	Cambial Initials			Tracheids		
	Max.	Mean	Min.	Max.	Mean	Min.
I. GINKGOALES						
1. Ginkgoaceae						
⁴ <i>Ginkgo biloba</i> L.....	3.0	2.2	1.4	2.9	2.2	1.4
II. CONIFERAE						
2. Taxaceae						
⁶ <i>Taxus cuspidata</i> Sieb. and Zucc.	1.6	1.1	0.8	1.7	1.3	0.8
3. Pinaceae						
(a) Abietaeae						
<i>Pinus Strobus</i> L.....	4.0	3.2	2.3	4.6	3.4	2.2
<i>Picea Abies</i> (L.) Karst.....	4.2	3.3	2.4	4.2	3.6	2.8
<i>Larix decidua</i> Mill.....	5.0	4.0	2.5	5.4	4.2	2.7
⁶ <i>Pseudotsuga taxifolia</i> (Lamb.) Britton.	1.6	1.2	0.7	1.8	1.2	0.9
⁶ <i>Abies Nordmanniana</i> Spach.....	1.5	1.1	0.7	1.8	1.2	1.0
⁶ <i>Cedrus libani</i> Barrel.....	2.6	2.0	1.2	2.7	2.1	1.3
⁶ <i>Tsuga canadensis</i> (L.) Carr.....	1.8	1.4	0.9	2.1	1.5	1.1
(b) Taxodieae						
⁶ <i>Sciadopitys verticillata</i> Sieb. and Zucc.	1.6	1.2	0.7	1.6	1.3	1.0
⁶ <i>Sequoia gigantea</i> Lindl. and Gord.....	4.5	3.7	2.5	4.5	3.8	2.8
(c) Cupresseae						
⁶ <i>Thuja occidentalis</i> L.....	2.1	1.5	0.7	2.4	1.7	1.3
<i>Juniperus virginiana</i> L.....	3.0	2.2	1.0	3.0	2.3	1.4

ANGIOSPERMAE-DICOTYLEDONEAE⁷

	Vessel-segments			Cambial Initials			Fiber Tracheids		
	Max.	Mean	Min.	Max.	Mean	Min.	Max.	Mean	Min.
A. ARCHICHLAMYDEAE									
I. SALICALES									
1. Salicaceae									
<i>Populus sp.</i>	0.70	0.50	0.19	0.66	0.49	0.35	1.19	0.90	0.61
II. JUGLANDALES									
2. Juglandaceae									
<i>Carya glabra</i> Sweet....	0.63	0.43	0.20	0.70	0.56	0.40	1.69	1.13	0.65
<i>Carya ovata</i> (Mill.) C. Koch.....	0.55	0.51	0.47	0.60	0.52	0.42	1.69	1.30	0.96
III. FAGALES									
3. Betulaceae									
<i>Alnus incana</i> (L.) Moench.....	0.84	0.66	0.43	0.72	0.60	0.34	1.20	1.89	0.56
<i>Betula populifolia</i> Marsh.....	1.17	0.89	0.65	1.16	0.94	0.70	1.60	1.31	0.91
4. Fagaceae									
<i>Quercus alba</i> L.....	0.60	0.46	0.36	0.67	0.53	0.39	1.42	1.00	0.80
IV. URTICALES									
5. Ulmaceae									
<i>Ulmus americana</i> L....	0.59	0.33	0.21	0.47	0.35	0.27	1.96	1.53	1.12
V. RANALES									
6. Trochodendraceae									
<i>Euptelea polyandra</i> Sieb. and Zucc.....	0.97	0.72	0.39	0.86	0.63	0.40	1.42	0.95	0.59
7. Annonaceae									
<i>Annona reticulata</i> L....	0.43	0.29	0.13	0.39	0.33	0.22	1.71	1.28	0.83

⁶ Material obtained from small branches or young stems.

⁷ Material obtained from stems of various ages.

TABLE I (Continued)

	Vessel-segments			Cambial Initials			Fiber Tracheids		
	Max.	Mean	Min.	Max.	Mean	Min.	Max.	Mean	Min.
<i>Phaeanthus ebracteolatus</i> Merr.....	0.58	0.39	0.23	0.61	0.44	0.27	1.40	0.94	0.61
8. Myristicaceae									
<i>Myristica philippensis</i> Lam.....	1.64	1.42	0.84	1.62	1.31	0.99	2.00	1.60	1.12
9. Lauraceae									
<i>Litsea glutinosa</i> C. R. Rob.....	0.74	0.52	0.36	0.70	0.55	0.39	1.49	0.95	0.56
<i>Sassafras officinale</i> Nees and Eberm....	0.50	0.39	0.22	0.50	0.39	0.27	0.83	0.61	0.38
VI. ROSALES									
10. Pittosporaceae									
<i>Pittosporum pentandrum</i> (Blanco) Merr.	0.90	0.66	0.29	1.01	0.80	0.56	1.22	0.99	0.76
11. Hamamelidaceae									
<i>Liquidambar styraciflua</i> L.....	1.39	0.76	0.41	0.98	0.70	0.40	1.75	0.96	0.67
12. Rosaceae									
<i>Pyrus Malus</i> L.....	0.72	0.51	0.29	0.74	0.53	0.34	1.29	0.98	0.61
<i>Prunus serotina</i> Ehrh..	0.58	0.45	0.23	0.59	0.46	0.32	1.40	0.99	0.58
<i>Pyrus</i> sp.....	0.80	0.57	0.44	0.77	0.66	0.52	1.17	0.92	0.59
13. Leguminosae									
<i>Robinia Pseudo-acacia</i> L.....	0.22	0.18	0.13	0.21	0.17	0.14	1.40	0.87	0.58
VII. GERANIALES									
14. Burseraceae									
<i>Canarium villosum</i> F. Vill.....	0.66	0.49	0.31	0.86	0.54	0.34	1.26	1.00	0.50
15. Meliaceae									
<i>Xylocarpus granatum</i> Koen. var.....	0.47	0.36	0.13	0.67	0.37	0.23	1.39	0.97	0.61
16. Euphorbiaceae									
<i>Excoecaria agallocha</i> L.	0.87	0.59	0.29	0.87	0.63	0.41	1.17	0.86	0.56
<i>Glochidion littorale</i> Bl..	1.28	0.90	0.36	1.21	1.04	0.72	1.84	1.52	0.92
VIII. SAPINDALES									
17. Anacardiaceae									
<i>Anacardium occidentale</i> L.....	0.56	0.42	0.27	0.70	0.44	0.25	0.88	0.66	0.47
<i>Buchanania arborea</i> Bl.	0.63	0.41	0.29	0.61	0.41	0.27	1.17	0.97	0.34
<i>Koordersiodendron pinatum</i> Merr.....	0.70	0.52	0.29	0.83	0.64	0.41	1.69	1.17	0.74
<i>Mangifera monandra</i> Merr.....	0.72	0.52	0.29	0.83	0.57	0.39	1.21	0.92	0.63
<i>Semecarpus cuneiformis</i> Blanco	0.52	0.29	0.25	0.56	0.43	0.29	1.12	0.79	0.54
18. Sapindaceae									
<i>Guioa Perrottetii</i> Bl....	0.45	0.38	0.32	0.66	0.43	0.25	2.00	1.48	0.96
<i>Sapindus saponaria</i> L. var. <i>Turczaninowii</i> Vidal	0.41	0.25	0.14	0.50	0.33	0.19	1.60	1.20	0.68
19. Aceraceae									
<i>Acer rubrum</i> L.....	0.64	0.49	0.27	0.61	0.49	0.32	1.24	0.84	0.50
IX. MALVALES									
20. Tiliaceae									
<i>Columbia serratifolia</i> DC.....	0.57	0.43	0.30	0.57	0.45	0.37	1.72	1.34	1.04
<i>Grewia multiflora</i> Juss.	0.34	0.25	0.14	0.37	0.25	0.16	1.09	0.75	0.48
21. Malvaceae									
<i>Thespesia populnea</i> (L.) Soland. ex Corr.	0.32	0.25	0.14	0.28	0.25	0.21	1.45	1.09	0.36

TABLE I (Concluded)

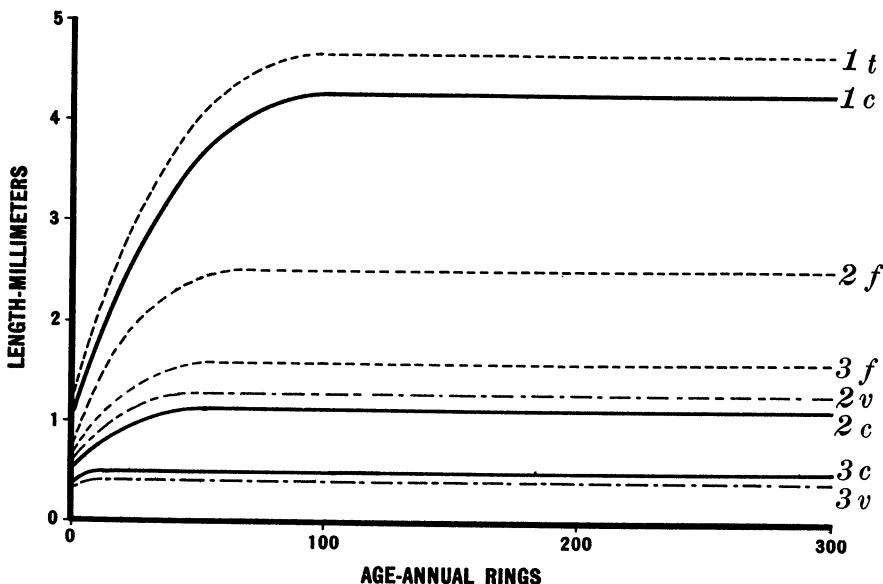
	Vessel-segments			Cambial Initials			Fiber Tracheids		
	Max.	Mean	Min.	Max.	Mean	Min.	Max.	Mean	Min.
22. Bombacaceae									
<i>Bombycidendron Vidalianum</i> Merr. and Rolfe	0.43	0.35	0.28	0.43	0.36	0.32	2.00	1.62	1.04
23. Sterculiaceae									
<i>Heritiera littoralis</i>									
Dryand.	0.37	0.31	0.25	0.36	0.30	0.27	1.88	1.42	0.96
<i>Kleinhovia hospita</i> L. .	0.50	0.33	0.19	0.48	0.36	0.27	1.24	0.89	0.52
<i>Pterospermum niveum</i>									
Vid.	0.50	0.37	0.19	0.43	0.37	0.30	1.90	1.48	0.77
<i>Sterculia foetida</i> L.	0.48	0.35	0.30	0.45	0.37	0.32	2.72	2.11	1.64
<i>Tarrietia sylvatica</i>									
Merr.	0.34	0.27	0.18	0.34	0.28	0.21	1.96	1.57	1.12
X. PARIETALES									
24. Guttiferae									
<i>Calophyllum Blancoi</i>									
Pl. and Tr.	0.99	0.61	0.36	0.90	0.59	0.41	1.35	0.96	0.54
<i>Garcinia dulcis</i> Kurz. .	1.24	0.80	0.48	1.09	0.80	0.52	2.88	2.01	1.12
<i>Garcinia</i> sp. (probably									
<i>lateriflora</i> Bl.)	1.04	0.78	0.48	1.02	0.74	0.52	2.52	1.88	1.28
25. Dipterocarpaceae									
<i>Anisoptera thurifera</i> Bl.	0.66	0.48	0.36	0.72	0.54	0.41	2.12	1.68	1.16
<i>Vatica Mangachapoi</i>									
Blanco.	0.79	0.58	0.36	0.81	0.61	0.41	1.63	1.15	0.61
XI. MYRTIFLORAE									
26. Lythraceae									
<i>Lagerstroemia speciosa</i> (L.) Pers.	0.43	0.30	0.18	0.50	0.33	0.21	1.52	1.08	0.64
27. Lecythidaceae									
<i>Barringtonia racemosa</i> (L.) Roxb.	0.97	0.68	0.39	0.90	0.72	0.50	3.84	2.51	1.20
28. Rhizophoraceae									
<i>Bruguiera parviflora</i>									
W. and A.	1.20	0.94	0.60	1.28	0.99	0.64	1.88	1.32	0.96
<i>Rhizophora</i> sp. (probably									
<i>Candelaria</i> DC.)	0.95	0.59	0.46	0.95	0.73	0.30	2.12	1.56	1.16
29. Nyssaceae									
<i>Nyssa sylvatica</i> Marsh.	1.72	1.25	0.88	1.27	0.83	0.54	2.52	1.76	1.16
XII. UMBELLIFLORAE									
30. Araliaceae									
<i>Shefflera odorata</i> Merr. and Rolfe	1.00	0.82	0.56	0.97	0.84	0.66	0.76	0.52	0.37
B. METACHLAMYDEAE									
XIII. CONTORTAE									
31. Oleaceae									
<i>Fraxinus americana</i> L.	0.48	0.31	0.18	0.37	0.29	0.18	1.38	0.96	0.54
XIV. RUBIALES									
32. Rubiaceae									
<i>Ixora philippinensis</i>									
Merr.	1.13	0.62	0.50	1.17	0.76	0.43	1.78	1.18	0.66
<i>Psychotria luzoniensis</i>									
F. Vill.	0.95	0.67	0.37	1.08	0.70	0.45	1.53	1.12	0.61

VARIATIONS IN CROSS-SECTIONAL AREA AND VOLUME

The variations in the length of cambial initials are not neutralized by concomitant changes in the radial and tangential diameters of the cells. On the contrary, the cross-sectional area of the elongated meristematic

cells tends to be somewhat larger in old than in very young stems, and in most gymnosperms than in dicotyledons. In other words, the basic fluctuations in *length* are paralleled by similar variations in *volume*.

The tracheary elements of the secondary xylem tend to increase in volume during differentiation. In the case of the tracheids of Coniferae this increase is due primarily to "radial" expansion and secondarily to elongation. The tangential diameter of the developing tracheids remains nearly constant. In arborescent and fruticose dicotyledons, on the other



TEXT FIG. 3. Normal length-on-age curves for cambial initials and tracheary cells in (1) typical conifer, (2) dicotyledon having primitive vessels, and (3) dicotyl having highly specialized vessels. *c*, cambium; *t*, tracheids; *f*, fiber tracheids; *v*, vessel-segments.

hand, the volume of fiber tracheids tends to be much influenced by elongation; and that of the vessel-segments by "tangential" as well as by "radial" expansion. As indicated by Sanio (1872) for *Pinus sylvestris* L., by Hartig and Weber (1888) for *Fagus sylvatica* L., and by Prichard and Bailey (1916) for *Carya ovata* (Mill.) K. Koch, the cross-sectional area and volume of tracheary cells tend to be larger in the outer than in the innermost growth layers of the stem. In gymnosperms, the changes in the volume of the tracheids in succeeding annual rings are closely dependent upon variations in the length and volume of the cambial initials, whereas, in many of the more highly specialized dicotyledons, the fluctuations in volume of the fiber tracheids and vessel-segments in various parts of the stem are due largely to changes which occur during the differentiation of the tracheary elements. In the dicotyledons as a group, the shortening of the cambial

initials and fiber tracheids—which is closely correlated with the development and specialization of vessels—results in a reduction in volume of these elements, but the decrease in length of the vessel-segments frequently is more than compensated for by an increase in their cross-sectional area. Thus, there is less contrast between the volume of the tracheids in gymnosperms and that of the vessel-segments in dicotyledons than there is between the size of the cambial initials in the two groups of plants.

SIGNIFICANCE OF SIZE VARIATIONS IN CAMBIUM AND XYLEM

These fundamental types of cell size variations, and concomitant fluctuations in form and structure, are significant in the investigation of a number of cytological, morphological, and physiological problems, as well as in the study of the identification and mechanical properties of timber, and will be discussed in greater detail in subsequent papers.

In view of the numerous factors or complexes of factors which affect the dimensions and volume of cells, it is not surprising that contradictory conclusions have been reached by different investigators who have attempted to generalize concerning cell size after limited induction. The data at hand indicate very clearly that the undifferentiated, actively dividing and growing cells of the lateral meristem or cambium may vary greatly in size in certain plants and remain relatively constant in others. Therefore, very different conclusions concerning the constancy of cell size or of cell number may be expected from intensive experimental investigations, depending upon the particular plant or portion of a plant which is selected for study. Similar discrepancies may be expected concerning body size and cell size. Depauperate plants (physiological dwarfs) frequently have smaller tracheary cells and cambial initials than individuals of normal stature, indicating a close correlation between cell size and body size. On the other hand, a large dicotyledon may be composed of much smaller cells than a small conifer or dicotyledon of similar age, suggesting that variations in cell size are independent of fluctuations in body size.

Sachs (1892, 1893, 1895) and Strasburger (1893) almost simultaneously called attention to the fact that undifferentiated, actively dividing and growing cells of plants, such as occur in embryonic and meristematic tissues, are relatively minute, and concluded that this is undoubtedly due to the fact that the working sphere of the nucleus is very restricted. Strasburger found that in terminal meristems the ratio between the average diameter of the nuclei and of the cells is as 0.003–0.16 mm.: 0.005–0.24 mm., or 2 : 3, and Sachs pointed out that, although plants vary enormously in their linear dimensions (0.001 mm. to 100 m.), the size of their constituent cells is relatively constant (0.001 to 0.05 mm.). Winkler (1916) reaches similar conclusions. He states that in meristematic somatic tissues the cells are of nearly uniform size and contain the diploid number of chromosomes, whereas in non-meristematic somatic tissues, in which multinucleate protoplasts, nuclear

fusions, and changes from the diploid to the tetraploid or polyploid condition are of frequent occurrence, many cells depart widely from the inherited, specific cell size of the plant. Therefore he suggests that there is a close correlation between cell size and chromosomal mass in both meristematic and non-meristematic somatic tissues.

Reconnaissance surveys of the higher plants indicate that the cambium should provide a favorable medium for testing the validity of these and similar generalizations concerning cell size, the working sphere of the nucleus, and the nucleo-cytoplasmic relation. Not only does the average size of the cambial initials fluctuate greatly in different groups of the Siphonogama, in different parts of a given individual, and in plants grown under different environmental conditions, but adjacent elements of the lateral meristem vary considerably in length, cross-sectional area, and volume. The cambial initials are of two distinct shapes and sizes: (1) numerous large, elongated cells, whose size variations have been described on preceding pages, and (2) scattered aggregations of small, more or less isodiametric elements which divide to form the horizontal sheets of radially disposed parenchyma, so-called medullary rays. The bulk of the divisions in both types of initials is periclinal, or parallel to tangents to the circumference of the stem or root. In other words, the large cells divide in a tangential, longitudinal plane which is a division plane of *maximal* area, whereas the ray initials form partition membranes that commonly are surfaces of *minimal* area. In gymnosperms and less highly differentiated dicotyledons, the cambium does not increase its periphery by radial, longitudinal divisions of the elongated initials and lateral enlargement of the products of such divisions. Instead, the cells elongate, sliding by one another, until they have attained a certain length. They then divide, by means of a pseudo-transverse partition, into two short halves which in turn elongate and divide.⁸ Owing to the fact that the initials do not elongate and divide (transversely) in unison, there is usually a very considerable variability in the length and *pari passu* in the volume of adjacent fusiform elements. However, the volume of the more or less isodiametric ray initials is very much less than that of even the smallest fusiform initials, and is of the same general order of magnitude as that of the undifferentiated cells of the embryo or terminal meristem. Therefore, in any particular portion of the cambium of these plants it is possible not only to study cell division and the nucleo-cytoplasmic relation in adjacent fusiform initials of very different lengths and volumes, but to contrast them with similar phenomena in adjoining ray initials, which resemble the cells of the terminal meristem in size and shape. Furthermore, by proper experimental methods, the fusiform initials may be induced to divide into small isodiametric units of the general order of magnitude of the ray initials or embryonic cells, and subsequently to regenerate elongated elements of normal dimensions.

⁸ During this process of elongation, between successive transverse divisions, the cells continue to divide in the tangential, longitudinal plane.

A number of interesting cytological problems suggest themselves in this connection. (1) Are the large, elongated initials multinucleate or hyperchromatic in conformity with the generalizations of Sachs, Strasburger, Winkler, and others? (2) Do the nuclei divide mitotically or amitotically? (3) What is the nature of cytokinesis in cells which are several hundred times as long as they are wide, and yet divide longitudinally? These and similar questions will be considered in the next paper of this series.

SUMMARY

1. Reconnaissance surveys of the higher plants reveal striking variations in the dimensions and volume of the cells of the cambium and secondary xylem.

2. Certain of the size variations are purely somatic, whereas others are germinal.

3. In many plants the dimensions and volume of tracheary cells are determined primarily by those of the cambial initials, whereas in others they are due largely to changes which occur during the differentiation of the xylem.

4. These fundamental types of size variations, and concomitant fluctuations in form and structure, are significant in the investigation of various cytological, morphological, and physiological problems.

5. The cambium appears to be an unusually favorable medium for the study of problems relating to cell size and body size, the working sphere of the nucleus, the nucleo-cytoplasmic relation, and phenomena of cytokinesis in somatic tissues.

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